

# Analysis of biological integrate-and-fire oscillators

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## Abstract

We consider discontinuous dynamics of integrate-and-fire models, which consist of pulse-coupled biological oscillators. A thoroughly constructed map is in the basis of the analysis. Synchronization of non-identical oscillators is investigated. Significant advances for the solution of second Peskin's conjecture have been made. Examples with numerical simulations are given to validate the theoretical results. Perspectives are discussed.

*Keywords:* Integrate-and-fire model, Pulse-coupling, Firing in unison, Coupling all-to-all, Periodic motions, Discontinuous dynamics.

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## 1. Introduction

The collective behavior of biological and chemical oscillators is a fascinating topic that has attracted a lot of attention in the last 50 years [1]-[28]. An exceptional place in the analysis belongs to synchronization, which in its general sense is understood as phase locking, frequency locking, and synchrony itself, that is motion in unison [1, 3],[5]-[33]. The integrate-and-fire model of the cardiac pacemaker [34] was developed by C. Peskin [35] to a population of identical pulse-coupled oscillators. It was conjectured that the model self-synchronizes such that:

- (C1) For arbitrary initial conditions, the system approaches a state in which all the oscillators are firing synchronously.
- (C2) This remains true even when the oscillators are not quite identical.

The conjecture (C1) is solved in [35] for a system with two oscillators, and in [21] for the generalized model of two and more oscillators. The last paper gave start to an intensive and productive investigation of the problem and its applications [7, 8, 23], [36]-[41]. As far as we know the conjecture (C2) remains unsolved. Even a developed non-identity concept has not been found in the literature.

In the present paper we generalize the model, and propose a version of non-identity. The model is considered such that perturbations save the synchronization. These oscillators are not only pulse-coupled, but connected during the time between moments of firing. That is, the modeling differential equations are not separated. One can see that this approach may provide more biological sense to this theory. The paper consists of main results, simulations and discussion of possible extensions. We believe that the results and proposals of this paper reveal new perspectives on the study of integrate-and-fire models of oscillators. The main role in our analysis is played by a specially defined map. It is not a Poincaré map, since it transforms the coordinate of one oscillator to that of another, and the two interchange roles in the course of the mapping. If there are more than two oscillators, they are used in pairs to shape the map with the interference of other oscillators acting as perturbation.

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The main object of our investigation is an integrate-and-fire model, which consists of  $n$  non-identical pulse-coupled oscillators,  $x_i, i = 1, 2, \dots, n$ . If the system does not fire the oscillators satisfy the following equations

$$x'_i = f(x_i) + \phi_i(x). \quad (1.1)$$

The domain consists of all points  $x = (x_1, x_2, \dots, x_n)$  such that  $0 \leq x_i \leq 1 + \zeta_i(x)$  for all  $i = 1, 2, \dots, n$ . When the oscillator  $x_j$  increases from zero, and meets the surface such that  $x_j(t) = 1 + \zeta_j(x(t))$ , then it fires,  $x_j(t+) = 0$ . This firing changes the values of all oscillators with  $i \neq j$ ,

$$x_i(t+) = \begin{cases} 0, & \text{if } x_i(t) + \epsilon + \epsilon_i \geq 1 + \zeta_i(x), \\ x_i(t) + \epsilon + \epsilon_i, & \text{otherwise.} \end{cases} \quad (1.2)$$

Thus, it is assumed that if  $x_i(t) \geq 1 + \zeta_i(x) - \epsilon - \epsilon_i$ , then the oscillator fires, too. It is assumed also that there exist positive constants  $\mu_i$  and  $\xi_i$  such that  $|\phi_i(x)| < \mu_i$  and  $|\zeta_i(x)| < \xi_i$ , for all  $x$  and  $i$ . In what follows, we call the real numbers  $\epsilon, \mu_i, \xi_i, \epsilon_i$ , *parameters*, assuming the first one is positive. Moreover, constants  $\xi_i, \epsilon_i, \mu_i$ , will be called *parameters of perturbation*. If all of them are zeros, then the model of identical oscillators is obtained. We assume that  $\epsilon + \epsilon_i > 0$ . That is, an excitatory model is under discussion. The function  $f$  is positive valued and lipschitzian. Moreover, assume that  $\zeta_i$  are continuous and  $\phi_i$  are locally lipschitzian for all  $i$ .

The coupling in the model is all-to-all such that each firing elicits jumps in all non-firing oscillators. If several oscillators fire simultaneously, then other oscillators react as if just one oscillator fires. In other words, any firing acts only as a signal which abruptly provokes a change of state. The intensity of the signal is not important, and pulse strengths are not additive. A system of oscillators is synchronized if all of them fire in unison.

In the present analysis we address synchronization as well as the existence of periodic solutions. Results that concern continuous and delayed couplings are considered in [42, 43].

We believe that the approach proposed in this paper will be useful for the investigation of a wide range of problems, focusing not only on synchrony and pulse-couplings, but also phase locking, frequency locking of systems, families of oscillators with continuous couplings. The method can be used to analyze inhibitory models as well as to evaluate the effects of coupling time deviations. Moreover, the model is suitable for the investigation of the existence of quasi-periodic and almost periodic motions.

## 2. The prototype map and two identical oscillators

In this section we shall define the map, which is the basic instrument of our investigation. It is constructed for a model more general, than is needed for this paper, to be the basis for future investigations.

Let us consider two identical oscillators,  $x_1(t), x_2(t), t \geq 0$ , which satisfy the following differential equations

$$x'_i = f(x_i), \quad (2.3)$$

where  $0 \leq x_i \leq 1, i = 1, 2$ . When the oscillator  $x_j$  fires at the moment  $t$  such that  $x_j(t) = 1, x_j(t+) = 0$ , then the value of another oscillator with  $i \neq j$ , changes so that

$$x_i(t+) = \begin{cases} 0, & \text{if } x_i(t) + \epsilon \geq 1, \\ x_i(t) + \epsilon, & \text{otherwise.} \end{cases} \quad (2.4)$$

Denote by  $u(t, 0, u_0)$ , the solution of the equation

$$u' = f(u), \quad (2.5)$$

such that  $u(0, 0, u_0) = u_0$ . Assume that the solution exists, is unique and continuable to the threshold for all  $u_0$ . Consider the solution  $u(t) = u(t, 0, v + \epsilon)$  of (2.5). Denote by  $s(v)$  the moment when  $u(s) = 1$ , and define the function  $\bar{L}(v) = u(s, 0, 0)$  on  $(0, 1 - \epsilon)$ .

The following conditions will be needed throughout the paper:

(A1)  $\bar{L}(v)$  is a strictly decreasing continuous function;

(A2)  $\eta = \lim_{v \rightarrow 0+} \bar{L}(v) > 1 - \epsilon$ ;

(A3)  $\lim_{v \rightarrow 1-\epsilon} \bar{L}(v) = 0$ .

Conditions (A1), (A3) are valid, if, for example,  $f$  is a positive and lipschitzian function. Another case will be considered in Example 2.3. It is obvious that there exists a unique fixed point,  $v^*, \bar{L}(v^*) = v^*$ .

Now, define a map  $L : [0, 1] \rightarrow [0, 1]$ , such that

$$L(v) = \begin{cases} \bar{L}(v), & \text{if } v \in (0, 1 - \epsilon), \\ \eta, & \text{if } v = 0, \\ 0, & \text{if } v \in [1 - \epsilon, 1]. \end{cases} \quad (2.6)$$

This newly defined function is continuous on  $[0, 1]$ . The sketch of its graph is shown in Figure 1. To make

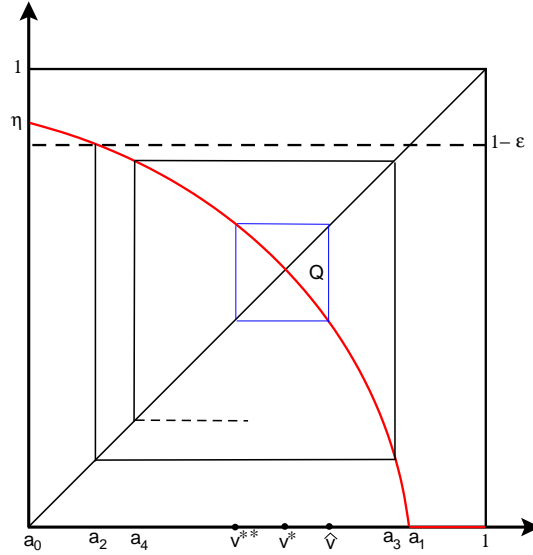


Figure 1: The graph of function  $w = L(v)$ , in red, and the period-2 orbit in blue. The points  $a_0 = 0, a_1 = 1 - \epsilon, a_{k+1} = L^{-1}(a_k), k = 1, 2, 3$ . (Color online)

the following discussion constructive consider the sequence of maps  $L^k(v), k = 1, 2, \dots$ , where  $L^k(v) = L(L^{k-1}(v))$  if  $k \geq 2$ . Their graphs with  $k = 1, 2, 3$  are shown in Figure 2. Denote  $a_0 = 0, a_1 = 1 - \epsilon, a_2 = L^{-1}(1 - \epsilon), a_3 = (L^2)^{-1}(1 - \epsilon), \dots$ . The sequence can be obtained also through iterations  $a_0 = 0, a_1 = 1 - \epsilon, a_{k+1} = L^{-1}(a_k), k = 1, 2, \dots$ , which are seen in Figure 1. It is clear that the sequences  $a_{2i}$  and  $a_{2i+1}$  are monotonic, increasing and decreasing respectively. One can verify existence of a fixed point  $v^{**} \leq v^*$  of the map  $L^2(v)$  such that  $\hat{v} = L(v^{**}) \geq v^*$ , and there are no fixed points of  $L^2$  in  $(0, v^{**})$ . Moreover,  $a_{2i} \rightarrow v^{**}$  and  $a_{2i+1} \rightarrow \hat{v}$  as  $i \rightarrow \infty$ . In the case  $v^{**} = v^*$ , there is no non-trivial period-2 points of  $L$ .

Let us show how iterations of  $L$  can be useful for the investigation of synchronization. Consider a motion  $(x_1(t), x_2(t))$  and a firing moment  $t_0 \geq 0$  such that  $x_1(t_0) = 1, x_1(t_0+) = 0, x_2(t_0+) = v, v \in [0, 1]$ .

**Lemma 2.1.** *Motion  $(x_1(t), x_2(t))$  synchronizes if and only if there exists a number  $k$  such that  $1 - \epsilon \leq L^k(v) \leq 1$ .*

**Proof.** Let us consider only necessity, since sufficiency is obvious. We shall consider the following two cases: (α)  $0 \leq v < 1 - \epsilon$ ; (β)  $1 - \epsilon \leq v \leq 1$ .

(α). It is clear that the couple does not synchronize at the moment  $t = t_0$ . While it is not in synchrony, there exists a sequence  $t_0 < t_1 < \dots$ , such that  $x_1$  fires at moments  $t_i$  with even  $i$  and  $x_2$  fires at  $t_i$  with

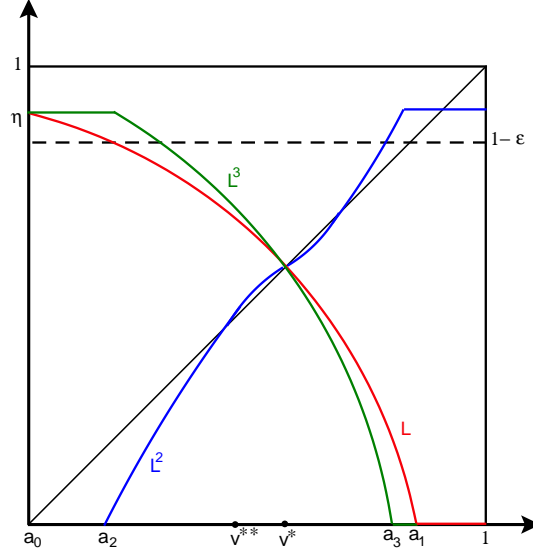


Figure 2: The graphs of  $L, L^2$  and  $L^3$  in red, blue and green respectively.(Color online)

odd indexes. Set  $v_i = x_1(t_i)$  if  $i$  is odd, and  $v_i = x_2(t_i)$  if it is even. Use the definition of  $L$  and identity of oscillators to obtain that  $v_{i+1} = L(v_i), i \geq 1$ . This demonstrates that map  $L$  evaluates alternatively the sequence of values  $x_1$  and  $x_2$  at firing moments.

The pair synchronizes eventually if and only if there exists  $k \geq 1$  such that  $x_1(t) \neq x_2(t)$ , if  $t \leq t_k$ , and  $x_1(t) = x_2(t)$ , for  $t > t_k$ . Both oscillators have to fire at  $t_k$ . That is,  $1 - \epsilon \leq v_k < 1$ .

( $\beta$ ). Consider  $1 - \epsilon \leq v < 1$ , as the case  $v = 1$  is primitive. We have that  $t_0$  is a common firing moment of both  $x_1$  and  $x_2$ , and it is the synchronization moment. Moreover,  $1 - \epsilon < L^2(x_2(t_1)) = \eta < 1$ . The lemma is proved.  $\square$

Thus, it is confirmed that the analysis of synchronization is fully consistent with the dynamics of the introduced map  $L(v)$  on  $[0, 1]$ , and, therefore,  $L$  can be used as a valuable tool in further investigation of the topic.

Let us consider the rate of synchronization. We solve the problem by indicating initial points which synchronize after precisely  $k, k \geq 0$ , iterations of the map. Denote by  $S_k$  the region in  $[0, 1]$ , where points  $v$  are synchronized after  $k$  iterations of map  $L$ . One can see that  $S_0 = [1 - \epsilon, 1]$ ,  $S_1 = [a_0, a_2]$ , and  $S_k = (a_{k-1}, a_{k+1}]$ , if  $k \geq 3$ , is an odd positive integer, and  $S_k = [a_{k+1}, a_{k-1})$ , if  $k \geq 2$ , is an even positive integer.

From the discussion made above it follows that the closer  $v$  is to  $v^{**}$  from the left or to  $\hat{v}$  from the right, the later is the moment of synchronization.

Denote by  $T$  the natural period of oscillators, that is, the period, when there are no couplings, and by  $\tilde{T}$  the time needed for solution  $u(t, 0, v^*)$  of (2.5) to achieve threshold. Since each oscillator necessarily fires within any interval of length  $T$  and the distance between two firing moments of an oscillator are not less than  $\tilde{T}$ , on the basis of the above discussion, the following assertion is valid.

**Theorem 2.1.** *Assume that conditions (A1) – (A3) are valid, and  $t_0 \geq 0$  is a firing moment such that  $x_1(t_0) = 1, x_1(t_0+) = 0$ . If  $x_2(t_0+) \in S_m, m$  is a natural number, then the couple  $x_1, x_2$  synchronizes within the time interval  $[t_0 + \frac{m}{2}\tilde{T}, t_0 + mT]$ .*

One can easily see that whenever condition (A2) is not valid, the system does not synchronize.

**Example 2.1.** *Consider the integrate-and-fire model of two identical oscillators  $x_1, x_2$ , with the differential equations*

$$x'_i = x_i^2 + c, \quad (2.7)$$

where  $i = 1, 2$ , and  $c$  is a positive constant. It is known [9] that the canonical type I phase model [4] can be reduced by a transformation to the form

$$u' = u^2 + c. \quad (2.8)$$

This time we investigate the model with the pulse-coupling.

Since the two equations are identical, we shall consider a solution  $u(t)$  of equation (2.8) to construct map  $L$ . We have that  $u(t, 0, v + \epsilon) = \sqrt{c} \tan(ct + \arctan(\frac{v+\epsilon}{\sqrt{c}}))$  and

$$\sqrt{c} \tan(cs + \arctan(\frac{v + \epsilon}{\sqrt{c}})) = 1. \quad (2.9)$$

Next,  $u(s, 0, 0) = \sqrt{c} \tan(cs)$ , and by applying (2.9) we find that

$$L(v) = c \frac{1 - v - \epsilon}{c + v + \epsilon},$$

if  $v \in (0, 1 - \epsilon)$ , and the fixed point is equal to  $v^* = \sqrt{(c + \epsilon/2)^2 + c(1 - \epsilon)} - (c + \epsilon/2)$ . Evaluate

$$L(0) = c \frac{1 - \epsilon}{c + \epsilon}$$

to see that  $L(0) < 1 - \epsilon$ , and condition (A2) is not valid. Moreover, one can verify that  $L'(v) < 0$ .

Thus, we obtain that the couple does not synchronize, and our simulations confirm this.

**Example 2.2.** Consider the following integrate-and-fire model of two identical oscillators,  $x_1, x_2$ , with the differential equations

$$x'_i = S - \gamma x_i, \quad (2.10)$$

where  $i = 1, 2$ , positive constants  $S, \gamma$  satisfy  $\kappa = \frac{S}{\gamma} > 1$ . One can find that  $u(t, 0, v + \epsilon) = (v + \epsilon)e^{-\gamma t} + \kappa(1 - e^{-\gamma t})$  and  $u(s, 0, 0) = \kappa(1 - e^{-\gamma s})$ . The last two expressions imply that

$$L(v) = \kappa \frac{1 - (v + \epsilon)}{\kappa - (v + \epsilon)}, \quad (2.11)$$

if  $0 < v < 1 - \epsilon$ .

There is a unique fixed point of  $L$  and  $L^2$ , and it is equal to

$$v^* = (\kappa - \frac{\epsilon}{2}) - \sqrt{\kappa^2 - \kappa + \frac{\epsilon^2}{4}}. \quad (2.12)$$

Finally,  $L(0) = \kappa \frac{1 - \epsilon}{\kappa - \epsilon} > 1 - \epsilon$ . That is, all conditions of the last theorem are valid, and the assertion in [35] is proved.

**Remark 2.1.** Map  $L$  is similar to that in [35], but the argument here is a coordinate before a jump, while in the paper the argument is a coordinate after a jump. This difference is not a critical one. The most important point is that C. Peskin uses it only as an auxiliary device to build the Poincaré map. We use  $L$  itself as the main map, with a newly defined continuous extension, which simplifies the discussion in this section and throughout our investigation. We revisit the problem of two identical oscillators, since  $L$  is the prototype map in our analysis. In addition to the main synchronization result, regions with equal time of synchronization are indicated, and the value of the fixed point,  $v^*$ , is evaluated.

**Example 2.3.** Consider the following integrate-and-fire system of pulse-coupled oscillators,  $x_1, x_2$ , such that

$$\begin{aligned} x_1' &= f(x_1), \\ x_2' &= f(x_2), \end{aligned} \quad (2.13)$$

where

$$f(s) = \begin{cases} 4 - 3s, & \text{if } 0 < s \leq 1/3; \\ 3, & \text{if } 1/3 < s \leq 2/3; \\ 4 - 3(s - 2/3), & \text{if } 2/3 < s \leq 1. \end{cases} \quad (2.14)$$

We have found that map  $L$  for this system exists and is equal to

$$L(v) = \begin{cases} \frac{2}{4-3v-3\epsilon}, & \text{if } 0 < v \leq 1/3 - \epsilon; \\ 1 - v - \epsilon, & \text{if } 1/3 - \epsilon < v \leq 2/3 - \epsilon; \\ \frac{4}{3} \frac{1-v-\epsilon}{2-v-\epsilon}, & \text{if } 2/3 - \epsilon < v \leq 1. \end{cases} \quad (2.15)$$

One can check that conditions (A1) – (A3) are fulfilled for this map. Moreover, the fixed points are equal to  $v^* = (1 - \epsilon)/2$ ,  $v^{**} = 1/3$  and  $\hat{v} = 2/3 - \epsilon$ . Finally, all the motions, which start outside of the periodic trajectory synchronize eventually, and all of them are periodic inside the trajectory.

The last example shows that the assumptions for map  $L$ , including the existence of the non-trivial period-2 motion, can be realized for even the differential equations with discontinuous right-hand side. Moreover, in future investigations one can consider isolated periodic solutions, stable or unstable. The theoretical consequences of this research are clear, if one uses the mappings theory, but construction of examples requires additional time.

**Example 2.4.** Consider the model of two integrate-and-fire identical oscillators,  $x_1, x_2$ , which are pulse-coupled and

$$\begin{aligned} x_1' &= S - \gamma x_1 + \beta x_2, \\ x_2' &= S - \gamma x_2 + \beta x_1, \end{aligned} \quad (2.16)$$

where constants  $S, \gamma$  and  $\beta$  are positive numbers. One can easily see that the system is the extended Peskin's model in Example 2.2. The terms with coefficient  $\beta$  are newly introduced in the system. They reflect the permanent influence of the partners during the process. Eigenvalues associated to (2.16) are  $\lambda_1 = -\gamma + \beta$  and  $\lambda_2 = -\gamma - \beta$ . We suppose that  $\beta$  is small so that both eigenvalues are negative. Moreover, it is assumed  $\kappa = S/\gamma > 1$ . Then,  $\kappa_1 = -S/\lambda_1 > 1$  if  $\beta$  is sufficiently small. The solution of system (2.16) with value  $(0, v + \epsilon)$  at  $t = 0$ , is equal to  $u_1(t) = \frac{1}{2}[e^{\lambda_1 t} - e^{\lambda_2 t}](v + \epsilon) - \kappa_1(e^{\lambda_1 t} - 1)$ ,  $u_2(t) = \frac{1}{2}[e^{\lambda_1 t} + e^{\lambda_2 t}](v + \epsilon) - \kappa_1(e^{\lambda_1 t} - 1)$ . By using these expressions obtain the equation  $\frac{1}{2}[e^{\lambda_1 s} + e^{\lambda_2 s}](v + \epsilon) + \kappa_1(1 - e^{\lambda_1 s}) = 1$ , and construct  $L(v) = 1 - (v + \epsilon)e^{\lambda_2 s}$ . Map  $L$  is too complex to analyze for properties (A1) – (A3). That is why we will compare this model with the couple in Example 2.2. The last two equations imply  $L(0) = \kappa \frac{1-\epsilon}{\kappa-\epsilon} > 1 - \epsilon$ , if  $\beta = 0$  and  $v = 0$ . That is, if  $\beta$  is sufficiently small, then condition (A2) is valid. We have found, also, by direct evaluations that the derivative  $L'(v)$  is negative if  $S$  and  $\beta$  are sufficiently large and small respectively. That is, condition (A1) is fulfilled. It is easy to verify that condition (A3) is also correct.

Now, using the continuity theorem in parameters [44], one can find that map  $L$  may admit a period-2 point only if the orbit is as close to the fixed point  $v^*$  of Example 2.2 as  $\beta$  is small. Consequently, the measure of the set of points, which can not be synchronized diminishes as  $\beta \rightarrow 0$ . This result is a new one. In previous papers the differential equations were separated.

### 3. The multidimensional system of non-identical oscillators.

Consider the model of  $n$  non-identical oscillators given by relations (1.1) and (1.2). The domain of this model consists of points  $x = (x_1, x_2, \dots, x_n)$  such that  $0 \leq x_i \leq 1 + \zeta_i(x)$  for all  $i = 1, 2, \dots, n$ .

Fix two of the considered oscillators, let say,  $x_l$  and  $x_r$ .

**Lemma 3.1.** Assume that condition (A2) is valid, and  $t_0 \geq 0$  is a firing moment such that  $x_l(t_0) = 1 + \zeta_l(x(t_0))$ ,  $x_l(t_0+) = 0$ . If parameters are sufficiently close to zero, and absolute values of parameters of perturbation sufficiently small with respect to  $\epsilon$ , then the couple  $x_l, x_r$  synchronizes within the time interval  $[t_0, t_0+T]$  if  $x_r(t_0+) \notin [a_0, a_1)$  and within the time interval  $[t_0 + \frac{m-1}{2}\tilde{T}, t_0 + (m+1)T]$ , if  $x_r(t_0+) \in S_m, m \geq 1$ .

**Proof.** Denote by  $x(t) = (x_1(t), x_2(t), \dots, x_n(t))$ , the motion of the oscillator. If  $1 + \zeta_r(x(t_0)) - \varepsilon - \varepsilon_r \leq x_r(t_0) \leq 1 + \zeta_r(x(t_0))$ , then these two oscillators fire simultaneously, and we only need to prove the persistence of synchrony which will be done later. So, fix another oscillator  $x_r(t)$  such that  $0 \leq x_r(t_0) < 1 + \zeta_r(x(t_0)) - \varepsilon - \varepsilon_r$ .

While the pair does not synchronize, there exists a sequence of moments  $0 < t_0 < t_1 < \dots$ , such that oscillator  $x_l$  fires at  $t_i$  with even  $i$ , and  $x_r$  fires at  $t_i$  with odd  $i$ . For the sake of brevity let  $u_i = x_l(t_i), i = 2j + 1, u_i = x_r(t_i), i = 2j, j \geq 0$ . In what follows we shall evaluate the difference  $u_{i+1} - L(u_i)$ .

Let us fix an even  $i$  and  $u_i = x_r(t_i)$ . If the parameters are sufficiently small, then there are  $k \leq n - 2$  distinct firing moments of the motion  $x(t)$  on the interval  $(t_i, t_{i+1})$ . Denote by  $t_i < \theta_1 < \theta_2 < \dots < \theta_k < t_{i+1}$ , the moments of firing, when at least one of the coordinates of  $x(t)$  fires, and  $v(t, t_0, v_0)$  the solution of the equation (1.1) with  $v(t_0, t_0, v_0) = v_0$ . We have that

$$\begin{aligned} x_r(\theta_1) &= x_r(t_i) + \epsilon + \int_{t_i}^{\theta_1} f(x_r(s))ds + \\ &\int_{t_i}^{\theta_1} \phi_r(x(s))ds, \end{aligned} \quad (3.17)$$

where  $x(t) = v(t, t_i, x(t_i+))$ ,

$$\begin{aligned} x_r(\theta_2) &= x_r(\theta_1) + \epsilon + \int_{\theta_1}^{\theta_2} f(x_r(s))ds + \\ &\int_{\theta_1}^{\theta_2} \phi_r(x(s))ds, \end{aligned} \quad (3.18)$$

where  $x(t) = v(t, \theta_1, x(\theta_1+))$ ,

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$$\begin{aligned} x_r(t_{i+1}) &= x_r(\theta_k) + \epsilon + \int_{\theta_k}^{t_{i+1}} f(x_r(s))ds + \\ &\int_{\theta_k}^{t_{i+1}} \phi_r(x(s))ds, \end{aligned} \quad (3.19)$$

where  $x(t) = v(t, \theta_k, x(\theta_k+))$ .

The moment  $t_{i+1}$  satisfies

$$1 + \zeta_r(x(t_{i+1})) - \epsilon - \epsilon_r \leq x_r(t_{i+1}) \leq 1 + \zeta_r(x(t_{i+1})). \quad (3.20)$$

Similarly to the expressions for  $x_r$  one can obtain

$$\begin{aligned} x_l(\theta_1) &= \int_{t_i}^{\theta_1} f(x_l(s))ds + \int_{t_i}^{\theta_1} \phi_l(x(s))ds, \\ x_l(\theta_2) &= x_l(\theta_1) + \epsilon + \int_{\theta_1}^{\theta_2} f(x_l(s))ds + \\ &\int_{\theta_1}^{\theta_2} \phi_l(x(s))ds, \end{aligned}$$

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$$x_l(t_{i+1}) = x_l(\theta_k) + \epsilon + \int_{\theta_k}^{t_{i+1}} f(x_l(s))ds + \int_{\theta_k}^{t_{i+1}} \phi_l(x(s))ds. \quad (3.21)$$

Formulas (3.17) to (3.21) define  $u_{i+1} = x_l(t_{i+1})$ . Similarly one can evaluate the number for odd  $i$ . Let us now find the value of  $L(u_i)$ . With this aim, evaluate

$$\phi(\bar{t}_{i+1}) = x_r(t_i) + \epsilon + \int_{t_i}^{\bar{t}_{i+1}} f(\phi(s))ds, \quad (3.22)$$

where  $\bar{t}_{i+1}$  satisfies  $\phi(\bar{t}_{i+1}) = 1$ , and

$$\psi(\bar{t}_{i+1}) = \int_{t_i}^{\bar{t}_{i+1}} f(\psi(s))ds, \quad (3.23)$$

to find that  $L(u_i) = \psi(\bar{t}_{i+1})$ . Next, we will show that the difference  $u_{i+1} - L(u_i)$  is small if the parameters are small.

First, one can find

$$\phi(t) - x_r(t) = \int_{t_i}^t [f(\phi(s)) - f(x_r(s))]ds - \int_{t_i}^t \phi_r(x(s))ds, \quad (3.24)$$

for  $t \in [t_i, \theta_1]$ .

Then, by applying the Gronwall-Bellman Lemma one can easily see

$$|\phi(\theta_1) - x_r(\theta_1)| \leq \mu_r(\theta_1 - t_i)e^{\ell(\theta_1 - t_i)}, \quad (3.25)$$

where  $\ell$  is the Lipschitz constant of  $f$ . Next, we have

$$|\phi(\theta_2) - x_r(\theta_2)| \leq [\mu_r(\theta_1 - t_i)e^{\ell(\theta_1 - t_i)} + \mu_r(\theta_2 - \theta_1) + \epsilon]e^{\ell(\theta_2 - \theta_1)}, \quad (3.26)$$

if  $t \in [\theta_1, \theta_2]$ .

Without loss of generality, assume that  $t_{i+1} > \bar{t}_{i+1}$ . Proceeding the evaluations made above, we can obtain  $|1 - x_r(\bar{t}_{i+1})| = |\phi(\bar{t}_{i+1}) - x_r(\bar{t}_{i+1})| = \Phi_1(\epsilon, \mu_r)$ , where

$$\begin{aligned} \Phi_1(\epsilon, \mu_r) \equiv & \mu_r[(\theta_1 - t_i)e^{\ell(\bar{t}_{i+1} - t_i)} + \sum_{j=1}^{k-1} (\theta_{j+1} - \theta_j)e^{\ell(\bar{t}_{i+1} - \theta_j)} + \\ & (\bar{t}_{i+1} - \theta_k)e^{\ell(\bar{t}_{i+1} - \theta_k)}] + \epsilon \sum_{j=1}^k e^{\ell(\bar{t}_{i+1} - \theta_j)}. \end{aligned}$$

There are positive numbers  $\mu$  and  $M$ , which satisfy  $\mu \leq f(s) \leq M$ , if  $0 \leq s \leq 1 + \max_i \xi_i$ . One can request the following inequality  $\max_{i=1, \dots, n} \mu_i < \mu$ . We have that  $|x_r(t_{i+1}) - x_r(\bar{t}_{i+1})| \leq |1 - x_r(t_{i+1})| + |1 - x_r(\bar{t}_{i+1})| \leq \Phi_1(\epsilon, \mu_r) + \xi_r$ . Consequently,

$$|t_{i+1} - \bar{t}_{i+1}| < \frac{\Phi_1(\epsilon, \mu_r) + \xi_r}{\mu - \mu_r} \equiv \Phi_2(\epsilon, \mu_r, \xi_r).$$



By applying (3.21) and (3.23), making similar evaluations for (3.25) and (3.26) one can find  $|\psi(\bar{t}_{i+1}) - x_l(\bar{t}_{i+1})| \leq \Phi_1(\epsilon, \mu_l)$ .

Then, we have that  $|u_{i+1} - L(u_i)| = |\psi(\bar{t}_{i+1}) - x_l(t_{i+1})| \leq |\psi(\bar{t}_{i+1}) - x_l(\bar{t}_{i+1})| + |x_l(t_{i+1}) - x_l(\bar{t}_{i+1})|$ , and, consequently,

$$|u_{i+1} - L(u_i)| \leq \Phi(\epsilon, \mu_r, \mu_l, \xi_r), \quad (3.27)$$

where  $\Phi \equiv \Phi_1 + \Phi_2(M + \mu_r)$ . It is obvious that  $\Phi$  tends to zero as the parameters do. This convergence is uniform with respect to  $u_0$ . We can also vary the number of points  $\theta_i$  and their location in the intervals  $(t_j, t_{j+1})$  between 0 and  $n - 1$ . The convergence also is indifferent with respect to these variations.

Consider the sequence of inequalities

$$|u_i - L^i(u_0)| \leq |u_i - L(u_{i-1})| + |L(u_{i-1}) - L(L^{i-1}(u_0))|, i = 1, 2, \dots$$

Then recurrently, by applying continuity of  $L$ , (3.27) and  $L^m(u_0) \in [1 - \epsilon, 1]$ , conclude that either  $1 + \xi_r - \epsilon - \epsilon_r \leq u_m < 1 + \xi_r$  or  $1 + \xi_l - \epsilon - \epsilon_l \leq u_{m+1} < 1 + \xi_l$ , if the parameters are sufficiently close to zero, and absolute values of the parameters of perturbation are sufficiently small with respect to  $\epsilon$ . Both of these inequalities bring the pair to synchronization.

Since each of the iterations of map  $L$  happens within an interval with length not more than  $T$ , we obtain that couple  $x_l, x_r$  synchronizes no later than  $t = t_0 + (m + 1)T$ . Similarly, the couple synchronizes not earlier than  $t = t_0 + \frac{m-1}{2}\tilde{T}$ .

If two oscillators  $x_l$  and  $x_r$  are non-identical and fire simultaneously at a moment  $t = \theta$ , how will they retain the state of firing in unison, despite being different? To find the required conditions, let us denote by  $\tau, \tau > \theta$  a moment when one of them, let's say  $x_r$ , fires. We have that  $x_l(\theta+) = x_r(\theta+) = 0$ . Then  $x_l(t) = x_r(t), \theta \leq t \leq \tau$ . It is clear that to satisfy  $x_l(\tau+) = x_r(\tau+) = 0$ , we need  $1 + \zeta_l(x(\tau)) - \epsilon - \epsilon_l \leq x_l(\tau)$ . By applying formula (3.20) again, this time with  $t_i = \theta, t_{i+1} = \tau$ , one can easily obtain that the inequality is correct if parameters are close to zero, and absolute values of the parameters of perturbation are sufficiently small with respect to  $\epsilon$ . Thus, one can conclude that if a couple of oscillators is synchronized at some moment of time then it persistently continues to fire in unison. The lemma is proved.  $\square$

**Remark 3.1.** The last lemma not only plays an auxiliary role for next main theorem, but can also be considered a synchronization result for the model of two non-identical oscillators.

Let us extend the result of the lemma for the whole ensemble.

**Theorem 3.1.** Assume that condition (A2) is valid, and  $t_0 \geq 0$  is a firing moment such that  $x_j(t_0) = 1 + \zeta_j(x(t_0)), x_j(t_0+) = 0$ . If the parameters are sufficiently close to zero, and absolute values of parameters of perturbation are sufficiently small with respect to  $\epsilon$ , then the motion  $x(t)$  of the system synchronizes within the time interval  $[t_0, t_0 + T]$ , if  $x_i(t_0+) \notin [a_0, a_1], i \neq j$ , and within the time interval  $[t_0 + \frac{\max_{i \neq j} k_i - 1}{2}\tilde{T}, t_0 + (\max_{i \neq j} k_i + 1)T]$ , if there exist  $x_s(t_0+) \in [a_0, a_1]$  for some  $s \neq j$  and  $x_i(t_0+) \in S_{k_i}, i \neq j$ .

**Proof.** Consider the non-trivial case. Applying the last lemma we can see that each pair  $(x_j, x_i), i \neq j$ , synchronizes within  $[t_0 + \frac{\max_{i \neq j} k_i - 1}{2}\tilde{T}, t_0 + (\max_{i \neq j} k_i + 1)T]$ . The theorem is proved.  $\square$

Now, replace coupling (1.2) by

$$x_i(t+) = \begin{cases} 0, & \text{if } x_i(t) + \epsilon + \epsilon_i \geq 1 + \zeta_i(x), \\ x_i(t) + \bar{\epsilon} + \epsilon_i, & \text{otherwise,} \end{cases} \quad (3.28)$$

where  $\bar{\epsilon}, \bar{\epsilon} + \epsilon_i > 0$ , is a new parameter, independent of  $\epsilon$ . Consider system (1.1) with (3.28). One can find that the following assertion is valid.

**Theorem 3.2.** Assume that condition (A2) is valid, and  $t_0 \geq 0$  is a firing moment such that  $x_j(t_0) = 1 + \zeta_j(x(t_0)), x_j(t_0+) = 0$ . If parameters  $\bar{\epsilon}, \mu_i, \xi_i, \epsilon_i$ , are sufficiently close to zero, then the motion  $x(t)$  of the system synchronizes within the time interval  $[t_0, t_0 + T]$ , if  $x_i(t_0+) \notin [a_0, a_1], i \neq j$ , and within the time interval  $[t_0 + \frac{\max_{i \neq j} k_i - 1}{2}\tilde{T}, t_0 + (\max_{i \neq j} k_i + 1)T]$ , if there exist  $x_s(t_0+) \in [a_0, a_1]$  for some  $s \neq j$  and  $x_i(t_0+) \in S_{k_i}, i \neq j$ .

We can see that (3.28) changes the style of interaction in the model. It depends on distance of oscillators to thresholds. We use this to introduce delay and continuous couplings in papers [42] and [43], respectively.

To illustrate Theorem 3.1, consider a group of oscillators,  $x_i, i = 1, 2, \dots, 100$ , with random uniform distributed start values in  $[0, 1]$ . It is supposed that they satisfy the equations  $x'_i = (3 + 0.01\bar{\mu}_i) - (2 + 0.01\bar{\zeta}_i)x_i$ . The constants  $\bar{\mu}_i, \bar{\zeta}_i$ , as well as  $\bar{\xi}_i$  in the thresholds  $1 + 0.005\bar{\xi}_i, i = 1, 2, \dots, 100$ , are uniform random distributed numbers from  $[0, 1]$ . In Figure 3 one can see the result of simulation with  $\epsilon = 0.08$ , where the state of the system is shown before the first, twenty first, forty second and sixty third firing of the system. So, it is obvious that eventually the model shows synchrony. Let us describe a more general system of oscillators

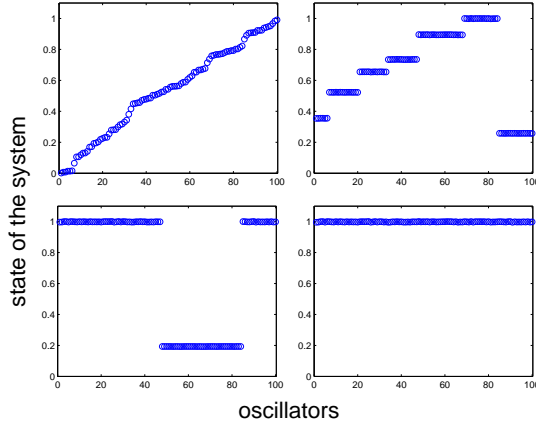


Figure 3: The state of the model before the first, twenty first, forty second and sixty third firing of the system. The flat sections of the graph are groups of synchronized oscillators.(Color online)

such that Theorem 3.1 is still true. A system of  $n$  oscillators is given, such that if  $i$ -th oscillator does not fire or jump up, then it satisfies the  $i$ -th equation of system (1.1). If several oscillators  $x_{i_s}, s = 1, 2, \dots, k$ , fire so that  $x_{i_s}(t) = 1 + \zeta_{i_s}(x)$  and  $x_{i_s}(t+) = 0$ , then all other oscillators  $x_{i_p}, p = k + 1, k + 1, \dots, n$ , change their coordinates by the law

$$x_{i_p}(t+) = \begin{cases} 0, & \text{if } x_{i_p}(t) + \epsilon + \sum_{s=1}^k \epsilon_{i_p i_s} \geq 1 + \zeta_{i_p}(x), \\ x_{i_p}(t) + \epsilon + \sum_{s=1}^k \epsilon_{i_p i_s}, & \text{otherwise.} \end{cases}$$

One can easily see that the last theorem is correct for the model just described, if  $\epsilon + \sum_{s=1}^k \epsilon_{i_p i_s} > 0$ , for all possible  $k, i_p$  and  $i_s$ .

**Remark 3.2.** *The analysis of non-identical oscillators with non-small parameters may shed light on the investigation of arrhythmias, chaotic flashing of fireflies, etc. Namely, the dynamics in the neighborhood and inside the periodic trajectory,  $Q$  in Figure 1, can be very complex. We do not exclude the possibility of chaos and fractals [40]. Bifurcation of periodic solutions can be discussed, if the parameters are small.*

#### 4. The Kamke condition and synchronization

In this section we consider an integrate-and-fire model with a new type of continuous connection.

We believe that models of identical oscillators with more general differential equations,

$$\begin{aligned} x'_1 &= g(x_1, x_2, \dots, x_n), \\ x'_2 &= g(x_2, x_3, \dots, x_1), \\ &\dots\dots\dots \\ x'_n &= g(x_n, x_1, \dots, x_{n-1}), \end{aligned} \tag{4.29}$$

where  $0 \leq x_i \leq 1, i = 1, 2, \dots, n$ , are of both theoretical and applied interest. The positive valued function  $g(y_1, y_2, \dots, y_n)$  in (4.29) is continuously differentiable and indifferent with respect to permutations of coordinates  $y_2$  to  $y_n$ .

When the oscillator  $x_j$  fires at the moment  $t$  such that  $x_j(t) = 1, x_j(t+) = 0$ , then the value of an oscillator with  $i \neq j$ , changes so that

$$x_i(t+) = \begin{cases} 0, & \text{if } x_i(t) + \epsilon \geq 1, \\ x_i(t) + \epsilon, & \text{otherwise.} \end{cases} \quad (4.30)$$

Consider the cone  $\mathbb{R}_+^n \subset \mathbb{R}^n$  of all vectors with nonnegative coordinates. Introduce a partial order in the cone such that  $a \leq b$  if  $a_i \leq b_i, i = 1, 2, \dots, n$ , [46].

We say that function  $g$  is of type  $\mathcal{K}$  in  $\mathbb{R}_+^n$  if  $a \leq b$  implies that  $g(a) \leq g(b)$ . The sufficient condition for that is  $\frac{\partial g(y)}{\partial y_i} \geq 0, i \neq 1$ .

Let  $u(t, t_0, u_0)$  and  $u(t, t_0, u_1), u_0, u_1 \in \mathbb{R}_+^n$ , be solutions of (4.29). If  $g$  is of type  $\mathcal{K}$ , then [45, 46] the dynamics of (4.29) is monotone for  $t \geq 0$ . That is,  $u(t, 0, u_0) \leq u(t, 0, u_1)$ , if  $u_0 \leq u_1$ .

Consider first the model of two oscillators. Define map  $L$  for this system in the following way. Take the solution  $u(t) = u(t, 0, (0, v + \epsilon)) = (u_1, u_2)$ . Denote by  $s(v)$  the moment when  $u_2(s) = 1$ , and define the function  $\bar{L}(v) = u_1(s)$  on  $(0, 1 - \epsilon)$ . Then define map  $L$  through (2.6). Let us check if conditions (A1), (A3) are valid for this map. Indeed, the continuity of  $\bar{L}$  is obvious. It is non-increasing since the monotonicity. Assume that there exist numbers  $v_1, v_2 \in (0, 1 - \epsilon)$  such that  $v_1 < v_2$  and  $s = s(v_1) = s(v_2)$ . Then, we have a contradiction as the open interval  $(v_1, v_2)$  is mapped to the closed set  $\{1\}$ . That is,  $\bar{L}$  satisfies (A1).

Condition (A3) is easily verifiable. Now, one can determine sets  $S_i$ , similarly to that in Section 2, and prove that the following theorem is valid.

**Theorem 4.1.** *Assume that  $g$  is of  $\mathcal{K}$  type, (A2) is valid, and  $t_0 \geq 0$  is a firing moment such that  $x_1(t_0) = 1, x_1(t_0+) = 0$ . If  $x_2(t_0+) \in S_m, m$  is a natural number, then the couple  $x_1, x_2$  synchronizes within the time interval  $[t_0 + \frac{m}{2}T, t_0 + mT]$ .*

We have, moreover, that, if  $g$  is of  $\mathcal{K}$  type and (A2) is not true then the system does not synchronize.

Consider the multidimensional system of oscillators. Introduce the function  $G(y, z) \equiv g(y, z, z, \dots, z)$ , and define the integrate-and-fire model of two identical oscillators  $y$  and  $z$  with the following system of differential equations

$$\begin{aligned} y' &= G(y, z), \\ z' &= G(y, z). \end{aligned} \quad (4.31)$$

Denote by  $u = (y, z), u(t) = u(t, 0, (0, v + \epsilon))$ , the solution of (4.31), and by  $s(v)$  the moment when  $z(s) = 1$ . Next, define the function  $\bar{L}(v) = y(s)$  on  $(0, 1 - \epsilon)$ . Then map  $L$  can be defined by (2.6) as well as correspond sets  $S_i$ . By applying the monotonicity of the dynamics, one can prove the following assertion, in a way very similar to that of Theorem 3.1.

**Theorem 4.2.** *Assume that  $0 \leq \frac{\partial g(y)}{\partial y_i} < \eta, i \neq 1$ , condition (A2) is valid, and  $t_0 \geq 0$  is a firing moment such that  $x_j(t_0) = 1, x_j(t_0+) = 0$ . If parameter  $\eta$  is sufficiently small then the motion  $x(t)$  of the system synchronizes within the time interval  $[t_0, t_0 + T]$ , if  $x_i(t_0+) \in S_0, i \neq j$ , and within the time interval  $[t_0 + \frac{\max_{i \neq j} k_i - 1}{2}T, t_0 + (\max_{i \neq j} k_i + 1)T]$ , if there exist  $x_s(t_0+) \in [a_0, a_1]$  for some  $s \neq j$  and  $x_i(t_0+) \in S_{k_i}, i \neq j$ .*

Example 2.4 shows that the analysis of the map  $L$  for Theorems 4.1 and 4.2 is not simple even with linear differential equations. The results of this section are therefore provided for numerical application, as well as for future investigations.

## 5. Conclusion

A version of the integrate-and-fire model of pulse-coupled and non-identical oscillators is investigated in this paper. We have made significant advances for the solution of second Peskin's conjecture, though we have

not showed that the measure of non-synchronized initial values is zero as it was shown in [21] for identical oscillators. However, we have located non-synchronized points, and showed that the time of synchronization infinitely increases as the region of points to be synchronized enlarges. Moreover, it is not necessary, in applications, for all points of the domain to fire in unison, and it is sufficient for the neighborhood of a motion to be synchronized.

A prototype map is introduced that helps to precise the results for a system of two identical oscillators and to solve the problem for the multi-non-identical-oscillators model. The approach of the paper is universal. For example, it can be applied if the thresholds are of the form  $1 + \phi(t, x)$  or  $1 + \phi(t)$ , which represents an oscillating signal in physiology [11] and a variation of the threshold of the electronic relaxation oscillator [32]. Moreover, the jump's value  $\epsilon$  as well as its perturbations may depend on  $x$ . The method can be easily extended for models, where differential equations have discontinuous right-hand sides, and only the existence of the map  $L$  with request properties are important to get appropriate results. Not only exhibitory, but inhibitory models of oscillators can be investigated, as well as delay of couplings [1, 7, 8, 42], and continuous couplings generated by firing [25, 43]. One can consider the models of our paper as discontinuous *cooperative* systems [46]. Consequently, we expect that by applying methods of dynamical systems with variable moments of discontinuity [47], the results on monotone systems [46, 48, 49] can be extended for these models.

There is a rich collection of results on oscillators, obtained through experiments and simulations. The approach of the present paper can give theoretical background for them and also form a basis for new ones. It can be applied not only to the problems of synchronization, but also to periodic, almost periodic motions, and the complex behavior of biological models. New small-world phenomena can be discovered. One can now request a certain property for the map  $L$  and then look for a system which meets the property. Thus, many new theoretical challenges can be brought under discussion. Conversely, if a system is given, then one can construct the corresponding map  $L$ , and by analyzing find new features which have not been mentioned in the present investigation.

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## 6. References

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